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Diversity and Distribution of Chars, Genus *Salvelinus*, in Northwestern North America in the Context of Northern Dolly Varden (*Salvelinus malma malma* (Walbaum 1792)).

Diversité et répartition des ombles, du genre Salvelinus, dans le nord-ouest de l'Amérique du Nord, par rapport au Dolly Varden (*Salvelinus malma malma* [Walbaum, 1792]).

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ABSTRACT

Four (or five) species of chars occur in waters of northwestern North America – Dolly Varden, Bull Trout, Arctic Char, Lake Trout, and Angayukaksurak Char. A sixth, Brook Trout, has been introduced in southern areas but does not co-occur with the above. The taxonomic differentiation of the first three of the above species is presently mostly resolved, however, past taxonomy has submerged or confused these taxa. Thus, over time the composition of populations within these taxa has varied which results in interpretive issues for earlier literature. Dolly Varden, Angayukaksurak Char and Bull Trout are all primarily associated with riverine habitats and the first two have been synonymised; although distinct, Bull Trout appear to be a species that exhibits similar ecological preferences but will use lakes for part of its life history if available. Arctic Char and Lake Trout are associated with lacustrine environments, although both use rivers for migrations and in some cases life history. Northern Dolly Varden and Bull Trout are generally parapatric, however, limited sympatry exists in the central Mackenzie River basin. Northern Dolly Varden and Arctic Char are mostly parapatric in Canada, and the few occurrences of the latter within the geographic range of the former are restricted to unconnected lakes; Arctic Char and Bull Trout are allopatric in distribution. Lake Trout, the most widely distributed char in this area, is sympatric with all other char species, however, ecological preferences appear to restrict contact. Accordingly, although possible based upon evidence from elsewhere, there are no documented cases of hybridization among the chars of northwestern Arctic North America. There is, however, implied introgression among some.

RÉSUMÉ

Quatre (ou cinq) espèces d'ombles vivent dans les eaux du nord-ouest de l'Amérique du Nord – le Dolly Varden, l'omble à tête plate, l'omble chevalier, le touladi et l'omble d'Angayukaksurak. Une sixième espèce, l'omble de fontaine, a été introduite dans les régions du sud, mais n'est pas présente aux mêmes endroits que les espèces ci-devant. La différentiation taxonomique des trois premières espèces est en grande partie résolue présentement; cependant, la taxonomie antérieure est venue jeter de la confusion entre les taxons. En effet, au fil du temps, la composition des populations de ces taxons a varié, ce qui a entraîné des problèmes d'interprétation de la littérature antérieure. Le Dolly Varden, l'omble d'Angayukaksurak et l'omble à tête plate sont principalement associés aux habitats fluviaux, et les deux premiers ont été considérés comme synonymes; bien que distincte, l'omble à tête plate semble afficher des préférences écologiques semblables, mais passe une partie de son cycle biologique dans des lacs lorsqu'il le peut. L'omble chevalier et le touladi sont associés aux environnements lacustres, bien que les deux emploient les cours d'eau pour les migrations et, dans certains cas, leur cycle biologique. Le Dolly Varden et l'omble à tête plate sont en général parapatriques; cependant, une sympatrie limitée existe dans le bassin central du fleuve Mackenzie. Le Dolly Varden et l'omble chevalier sont la plupart du temps parapatriques au Canada, et les quelques occurrences de l'omble chevalier dans l'aire de répartition géographique du Dolly Varden sont limitées à des lacs non reliés; l'omble chevalier et l'omble à tête plate affichent quant à eux une répartition allopatrique. Le touladi, qui est l'omble ayant la plus vaste aire de répartition dans ce secteur, est sympatrique de toutes les autres espèces d'ombles, mais les préférences écologiques semblent limiter les contacts. En conséquence, bien que l'hybridation soit possible d'après des preuves recueillies ailleurs, aucun cas n'a été documenté entre les ombles du nord-ouest arctique de l'Amérique du Nord. Cependant, une introgression implicite existe entre certains ombles.

1.0. INTRODUCTION

Fishes of the genus *Salvelinus* present a confusing array of diversity and variation at many taxonomic levels. This diversity combined with generally poor sampling of northern areas has led to the description of numerous taxonomic forms. Most of these have been described as formal species at one time or another. Moreover, populations or groups in particular geographic areas have been aligned with formal species in many different ways by taxonomists. Thus, two problems are inherent within the taxonomy of chars from northwestern North America: 1) What species are actually present and can be accepted as such on formal taxonomic grounds, and, 2) What is the presently understood composition within those species? Reasonably sound answers to these two questions then raise two additional issues of relevance in the context of status assessments for the species. 3) What are the distributions of the species (or other formal taxa)? And, 4) in areas where the distributions abut or overlap what is the potential for hybridization (i.e., present-day interbreeding) and/or the evidence for introgression (i.e., successful past interbreeding events which have resulted in genetic exchange among taxonomic lineages)?

The objective of this report is to outline the present, most-resolved view and consensus opinion regarding the taxonomic diversity of chars in northwestern North America, and to provide updated distributional information for these taxa. Although presented herein as current, resolved understanding, the reader is reminded that a) some experts will have differing opinions, b) unresolved situations abound in char taxonomy, c) these views are tested and supported hypotheses based upon best evidence but as such are subject to change, and, d) continued sampling will further test these views. The strength of the hypotheses of taxonomic diversity thus lies in their ability to accommodate new information. This summary is presented as a background within which further examination of the diversity of Dolly Varden (*Salvelinus malma* (Walbaum 1792)) can be conducted. The general geographic area of focus is northern British Columbia (BC), Alberta (AB), Alaska (AK), Yukon Territory (YT) and the western Northwest Territories (NT), i.e., 'northwestern North America'. The specific geographic focus is the lower Mackenzie River basin, Peel River basin, and the north slope of the Yukon Territory.

2.0. CHARS PRESENT IN NORTHWESTERN NORTH AMERICA

Using presently accepted species-level taxonomy, five (or six) species of chars of the genus *Salvelinus* are present in North America and four (or five) of these are most relevant to the area considered here. The American Fisheries Society (Nelson *et al.* 2004) formally recognizes the following species, arranged here in order of importance to the status assessment of Dolly Varden in northern Canada: 1) *Salvelinus malma* (Walbaum 1792), Dolly Varden (DVCH); 2) *Salvelinus confluentus* (Suckley 1859), Bull Trout (BUCH); 3) *Salvelinus alpinus* (Linneaus 1758), Arctic Char (ARCH); 4) *Salvelinus namaycush* (Walbaum 1792), Lake Trout (LKCH); and, 5) *Salvelinus fontinalis* (Mitchill 1814), Brook Trout (BKCH). 6) An additional char form of uncertain taxonomic status at the species level has been described and may be relevant to Dolly Varden assessments (see below) – *Salvelinus anaktuvukensis* Morrow 1973, Angayukaksurak char (or Old Man char) (ANCH).

3.0. CHARS IN THE CONTEXT OF OTHER FISHES

Chars are members of the family Salmonidae which is presently considered to be the only family within the Order Salmoniformes (Nelson 1994); however, ordinal status and relationships

are unresolved at present. Salmonids are freshwater and anadromous fishes found throughout the northern hemisphere characterized by Nelson (1994) as follows: a) deep posterior myodome with eye musculature passing through and attaching to trunk musculature, b) adipose fin present; c) mesocoracoid present; d) gill membranes extending far forward and free from isthmus; e) pelvic axillary process present; f) last three vertebrae upturned; g) 11-210 pyloric caecae; h) 7-20 branchiostegal rays; i) 50-75 vertebrae; j) tetraploid karyotype; k) parr marks present in young of most; and, l) variable size to ~ 1.5 m in length. Most studies suggest there are three subfamilies (but this is unresolved) among which eleven genera and about 66 species are found. [Note: Definition of what constitutes a species for freshwater fishes is a subject of major contention, and salmonids are extreme examples of highly variable and thus problematic taxa for defining such. Thus, depending upon one's perspective of a 'species' for salmonids and whether the emphasis is upon classical character suites such as morphology, upon genetics, or upon ecological roles, the number of species which can be logically argued varies widely. Chars as a genus represent the range of extremes found within salmonids.]

Following Nelson (1994), the three subfamilies and their composition are as follows: 1) Coregoninae – whitefishes and ciscoes – with three genera and about 32 species; 2) Thymallinae – graylings – one genus with four or five species; and, 3) Salmoninae – taimens, chars, Atlantic and Pacific trouts, and Pacific salmons – seven genera with about 30 species. *Salvelinus*, the genus of chars, is composed of three formally recognized sub-genera: a) *Salvethymus* with one species (endemic to one location in Chukotka); b) *Baione* with two North American species, Brook Trout and Lake Trout; and, c) *Salvelinus* with about eight (or many more – see note above) species distributed holarctically with one present in northern-most freshwater environments. Dolly Varden as a species belongs to the latter sub-genus. Taxonomy of Dolly Varden below the species level is not addressed herein, rather is the subject of a separate report (Kowlachuk *et al.* 2010).

4.0. FULL TAXONOMIC ASSOCIATION OF DOLLY VARDEN

Following Nelson (1994) the taxonomic association of Dolly Varden is as follows:

Phylum Chordata
Subphylum Vertebrata
Superclass Gnathostomata
Grade Teleostomi
Class Actinopterygii
Subclass Neopterygii
Division Teleostei
Subdivision Euteleostei
Superorder Protacanthopterygii
Order Salmoniformes
Family Salmonidae
Subfamily Salmoninae
Genus *Salvelinus*

5.0. CHAR SPECIES AND COMPOSITION IN NORTHWESTERN NORTH AMERICA

As noted above, taxonomic confusion exists at two levels within *Salvelinus* – the number of species present and the composition of various sub-specific taxa (including populations) of those species. In the present context, this issue is best approached sub-regionally within northwestern North America – thus presently accepted taxonomy and composition of the species will be considered in two geographic contexts, both of which link directly to the assessment of Dolly Varden: 1) northern coastal and freshwater Yukon and Northwest territories; and, 2) interior southern freshwaters of the Mackenzie River basin.

1) Alaska and northern coastal and freshwater areas of the Yukon and Northwest territories

Three described taxa of chars are most relevant in this area: Dolly Varden, Arctic Char and Angayukaksurak Char. In areas of southwestern Alaska, two taxa (Dolly Varden and Arctic Char) are present both sympatrically (i.e., occur in the same area) and syntopically (i.e., occur in the same water body). These are morphologically and ecologically distinct and distinguished by pyloric caecae and gill raker counts – high in Arctic Char and low in Dolly Varden (DeLacy and Morton 1943, McPhail 1961). Generally Arctic Char tends to be a lacustrine fish and non-migratory in northwestern North America, whereas Dolly Varden utilizes rivers as primary habitats and often is migratory to/from marine areas (i.e., anadromous). Elsewhere in this area (e.g., Seward Peninsula of western Alaska, north slope drainages of Alaska and the Yukon Territory), Dolly Varden and Arctic Char may be sympatric but not syntopic (see distribution notes below).

Syntopy combined with no (or very low) hybridization is (and was) taken as *prima facie* evidence that the two taxa were distinct at the species level (McPhail 1961). Subsequent investigation of additional populations and characters, particularly genetic parameters confirm this view (Reist *et al.* 1997; Reist unpubl. data, Taylor *et al.* 2008), despite some views to the contrary (Brunner *et al.* 2001). Thus, with respect to species-level distinctness, Dolly Varden and Arctic Char are considered herein to be 'good' species. The composition and distribution of these have differed among studies and continue to evolve as understanding grows; these compositional and distributional differences have influenced assessments and management. Thus, for Dolly Varden, McPhail (1961) suggested three taxa: a) a northern form with more vertebrae and gill rakers which occurred north of the Alaska Peninsula to the Seward Peninsula of western Alaska; b) a southern form (fewer vertebrae and gill rakers) occurred in the Aleutian Islands and areas south of the Alaska Peninsula extending to British Columbia and further southwards; and c) a distinct inland form with low counts of pyloric caecae occurred in central Alaskan inland drainages (McPhail 1961). For Arctic Char, McPhail (1961) also suggested three taxa as follows: a) a Bering Sea-western Arctic form with fewer pyloric caecae and gill rakers distributed from the lower Kuskokwim River (Alaska) north and east to the lower Mackenzie River basin of Canada; b) east of the Mackenzie basin an eastern form of Arctic Char possessed higher counts for these characters; and c) a Bristol Bay-Gulf of Alaska form occurring south of the Kuskokwim River resembled the eastern form of Arctic Char.

Following this structure, two forms of char co-occurring in the Sagvanirktok River of north slope Alaska were equated to the Bering Sea-western Arctic and eastern forms of Arctic Char (McCart and Craig 1971). Morrow (1973) described the Angayukaksurak Char as a distinct species found in north-flowing extreme head water streams of the Brooks Mountains of northern Alaska. Morphological and particularly ecological (i.e., putative spring-spawning) characters provided the evidence of distinctness, and the species was viewed as being closely allied to Dolly Varden (Morrow 1973).

Thus, to about 1980, the prevailing view was that various forms of Arctic Char were the only char taxa present in extreme northern locations along the north slope of Alaska eastwards to the Mackenzie Basin, however, locally distinct chars could be found in some isolated locations. Re-examination of the taxonomy of chars from the Prudhoe Bay area of north slope Alaska east to the Mackenzie River by McCart (1980) realigned this. First, the status of the Angayukaksurak char as a distinct species was questioned and concluded to be a variant form of Dolly Varden (Morrow 1980). Second, only two forms of chars were thought to be present in this area: all stream-resident and isolated stream-resident populations (and a single Alaskan lake population) were viewed as Arctic Char (i.e., the Bering Sea-western Arctic form of McPhail (1961)). All remaining lake populations of char of uncertain affinities found in this area were eastern form Arctic Char. Morrow (1980) using multivariate morphology re-examined this issue from the perspective of Alaskan chars and concluded that: a) all lake-resident char in southern Alaska were distinct from both southern and northern forms of Dolly Varden (*sensu* McPhail 1961), b) these latter two almost completely overlapped, and, c) the Bering Sea-western Arctic form of Arctic Char completely overlapped the northern form of Dolly Varden.

Thus, with the Angayukaksurak Char submerged with Dolly Varden, two species-level taxa are present in this area, however, the composition of these has differed over recent time periods. Prior to 1980, populations of riverine-resident chars from north slope locations west of the Mackenzie River are considered as a form of Arctic Char; from 1980 onwards evidence suggests these are in fact a form of Dolly Varden similar to those found in western coastal Alaskan rivers.

Therefore to about the mid-1980s, three taxonomic forms of char are present in northwestern North America and considered most likely to represent two species. Char from lacustrine habitats west of the Mackenzie River appear to be, with one exception, Arctic Char. Char from riverine habitats south of the Alaska Peninsula are viewed as Dolly Varden (likely southern form). However, char from riverine habitats north of the Alaska Peninsula throughout western Alaska and the continental north slope east to the Mackenzie River were viewed as either being a form of Dolly Varden or Arctic Char depending upon which authority was followed. Nomenclatural usage for chars in studies from this region from 1980 to the 1990s reflects this confusion. Thus, careful examination of the literature from this period is required to accurately determine the species under consideration and to ensure data and assessments reflect the proper taxon.

Reist *et al.* (1997) re-examined char taxonomy for northwestern North America and concluded the following: a) riverine char and lacustrine char from north slope areas west of the Mackenzie River are different at the species level, b) lacustrine fish in this area are a form of Arctic Char, and, c) riverine fish are a form of Dolly Varden. The latter includes the semi-anadromous (i.e., sea-run) life history type and the co-occurring riverine-resident (residual) type, as well as stream-resident types isolated above impassable barriers or by inland distances (see Sawatzky and Reist in prep.). Although taxonomic studies for chars from this area have not been recently pursued, all additional evidence which has been accumulated (e.g., morphological evidence

from additional sampling of previous and new populations, genetic evidence from mitochondrial DNA, and to a limited degree genetic evidence from nuclear DNA, Reist unpubl. data), all agree with these conclusions. Recent examination of the specific status and the affinity of the Angayukaksurak Char has not occurred; thus, the conclusions of Morrow (1980) remain (i.e., it is viewed as a distinct ecological type within Dolly Varden (Nelson 1994) until shown otherwise).

Although considered herein as distinct and valid taxa at the species' level, as noted previously some authors do not consider Dolly Varden and Arctic Char to be species (e.g., Brunner *et al.* 2001). This combined with the following: a) high levels of morphological and ecological diversity in both forms (i.e., life history variants, ecological types and morphological types all exhibiting varying degrees of genetic differentiation), b) wide range of numerous closely allied 'good' species (or at least taxa described as such) in Eurasia, and, c) contradictory and ambiguous evidence from different character systems and from different geographic regions, all have been used to argue that all Arctic Char and their closely allied forms, and all Dolly Varden and their closely allied forms represent one unresolved species complex – the 'Arctic Char species complex'. That view is not followed herein given the arguments presented above particularly for these taxa within North America where they appear to be clearly differentiated (e.g., see Taylor *et al.* 2008).

2) Southern freshwater taxonomic and compositional confusion

Similar to the situation described above for the northern areas of Dolly Varden distribution, chars in fresh waters from the southern Mackenzie River basin present confusion with respect to taxonomy, composition and distribution. This confusion exists for identification of chars within the Mackenzie River and its tributaries from the southern Yukon and Northwest Territories in both lacustrine and riverine environments. Three species of chars are involved – Arctic Char, Dolly Varden and Bull Trout. In older literature (i.e., prior to ~2000) summarizing work in this area, chars present in rivers of the area were variously identified as Arctic Char (i.e., typically prior to the mid 1980s) or Dolly Varden (i.e., mid 1980s to ~2000). Further confusion exists in that two distinct species of chars, Bull Trout and Dolly Varden were combined into the latter taxon until clarification by Cavender (1978); taxonomic resolution and identifications for these two in the more northerly areas of their distribution (i.e., BC, AB and YT) was addressed by Haas and McPhail (1991). Until Reist *et al.* (2002), this situation remained unresolved in the upstream portions of the Mackenzie River basin. Reist *et al.* (2002) examined both old records identified as Arctic Char and/or Dolly Varden and new specimens of chars from the mainstem Mackenzie and side tributaries, and concluded that all previous reports of chars south of the Great Bear River were almost certainly Bull Trout and that the new specimens represented this species. Based upon existing data, samples and understanding, Arctic Char was ruled out as occurring within the Mackenzie Basin (with the occasional possible exception of vagrant individuals found at exceedingly low frequencies – see below). Moreover, in the Mackenzie River basin the downstream distribution of Bull Trout (i.e., the northern-most extent) and the upstream distribution (i.e., the southern-most extent) of Dolly Varden were shown to be uncertain and predicted by Reist *et al.* (2002) to possibly abut (i.e., be parapatric) or overlap (i.e., be sympatric) in the poorly sampled areas of the Sahtu Settlement Region. Work since that time (e.g., Mochnacz *et al.* 2004, Mochnacz and Reist 2007) has confirmed the widespread presence of Bull Trout throughout much of the Deh Cho and Sahtu areas. Additional work (Mochnacz *et al.* 2009) has also confirmed sympatry and limited syntopy of Bull Trout and Dolly Varden in the Gayna River (65°17'N; 129°21'W). Sampling in 2007 and 2008 found that these two species, although occurring together in the same river system are generally not syntopic, with the Bull Trout occupying downstream areas connected to the Mackenzie mainstem (and possibly migratory) and the Dolly Varden isolated above barriers and thus non-migratory. However, at least one capture of a Dolly Varden in the downstream location (i.e., syntopic with

Bull Trout) suggests some individuals may be washed downstream (Mochnacz *et al.* 2009) with unknown consequences for species' integrity. Similar to the cautions made above, careful examination of the literature (and where necessary re-assignment of species identities) is required for chars identified as Arctic Char and Dolly Varden throughout this area prior to 2002; ideally voucher specimens of chars from throughout these areas should be taken and identified by qualified experts, and confirmed using diagnostic criteria such as genetics.

A final char taxon present in this area, Lake Trout, although sympatric with the other three species and syntopic in many locations appears to present little taxonomic problems both as a species (i.e., from the compositional perspective) and with respect to distributional issues. Thus, other than general information of potential relevance (e.g., distribution and notes on potential hybridization) this species is not considered further.

6.0. GENERAL DISTRIBUTIONS OF CHAR SPECIES IN THE AREA

With the taxonomic issues and compositions developed above in mind, the general distributions of char species in northwestern North America can be developed. These summaries represent our most up-to-date understanding but are subject to change as new information becomes available, particularly in poorly sampled regions such as high elevation streams in the lower Mackenzie and Peel river basins.

6.1. NORTHERN DOLLY VARDEN (FIGURE 1)

Northern Dolly Varden (see Kowalchuk *et al.* 2010 for complete taxonomic delineation of this subspecies) are present as anadromous (i.e., sea-run) fish in coastal waters of the Beaufort Sea in the western Arctic primarily west of the Mackenzie Delta during ice-off periods (i.e., summer and early autumn). Offshore distribution is poorly known mostly due to poor sampling effort, however, present understanding suggests Dolly Varden primarily occur in nearshore waters within the 0 - 10 m isobaths. Occasional offshore feeding forays into surface waters over deeper depths may occur where oceanographic conditions are suitable (i.e., partially freshened and warm water), but this is generally undocumented. Dolly Varden found in these marine areas include any smoltified (i.e., physiologically transformed to survive in marine waters) fish including large juveniles (i.e., not yet mature fish) and adults (i.e., maturing or matured fish) (see Sawatzky and Reist in prep. for life history descriptions). All such individuals tend to have dark dorsal colouration and silvery sides with white bellies; that is, the spectacular red, green, black and white colouration characteristic of breeding adults is not exhibited while fish are in marine habitats. In highly freshened deltas and nearshore areas, small pre-smolt juveniles may also occur which geographically may be considered marine but which ecologically are extensions of freshwater habitats. The structuring (i.e., size, age or life stage groupings) of Dolly Varden while in the Beaufort Sea is poorly known, however, generally larger fish will be found further away from their natal systems than will smaller fish. Dolly Varden are the only char species in this area which exhibits anadromy by moving away from deltas and into high saline areas, thus confused identifications should not occur for fish sampled from marine systems (note that if present in the system, some Lake Trout may seasonally be found in nearshore deltas where rivers enter the sea).

The distribution of Dolly Varden in fresh waters in the northwestern Canadian Arctic is restricted to habitats which provide for spawning, overwintering and rearing. As noted previously, ecologically northern Dolly Varden are primarily a taxon adapted to flowing waters, thus high-gradient rivers in this area are their primary habitats. Populations are found year round in

association with rivers in this area which have perennial groundwater inputs that provide spawning and overwintering habitat (see Stewart *et al.* 2010 for detailed habitat information); seasonal utilization of ephemeral connected streams is also likely (but individuals doing so must return to the groundwater-fed reaches to survive winter as other reaches freeze solid). Anadromous individuals use groundwater-fed habitats seasonally for reproduction and overwintering depending upon life stage, whereas all stages of pre-smolt fish and also residual life history types remain in such areas year round. Some utilization of other unconnected ephemeral streams present on the Yukon North Slope presumably by anadromous fish (e.g., possibly for summer feeding) has been documented, however, this is minimal and individuals doing so must migrate back to groundwater-fed systems to survive winter. Populations isolated by barriers such as falls and/or by distance from the sea similarly are associated with high-gradient streams fed by significant groundwater inputs. No locations in northwestern Arctic Canada are known where northern Dolly Varden occupy lakes, however, this is documented in one location in north slope Alaska (Mecklenburg *et al.* 2002) but this requires confirmation. They may also occupy lakes in more inland areas (see below).

Dolly Varden, presumably representing the northern subspecies, are found in inland locations in mountain rivers draining into the west side of the Mackenzie River and in the Peel River basin. These all appear to represent isolated populations however those closer to the Beaufort Sea may contain individuals that exhibit anadromy. Such populations are incompletely surveyed at present – the furthest known upstream location (and presently the only known site upstream of Point Separation in the Mackenzie Delta) in the Mackenzie River basin is that of the Gayna River described above. In the Peel River basin, isolated populations of Dolly Varden appear to be moderately frequent and are likely much more widespread than presently documented. Virtually all these are isolated by either distance or barriers. Populations in the upper Peel River basin are of uncertain affinities – i.e., possibly of the northern taxon or perhaps representative of the interior isolated form hypothesized to occur in upstream areas of the Yukon River basin in Alaska. Such fish tend to be morphologically and genetically distinct from the northern form to some degree (Groening 2008, Reist unpubl. data), and research addressing this issue is underway. Some populations in this area may also occur in lakes at higher elevations (Bodaly and Lindsey 1977; Mann and Tsui 1977; Yukon Department of Environment 2000 unpubl.; Yukon Department of Environment 2004 unpubl. cited in Anderton 2006; Reid and Skinner 2008).

Southern Dolly Varden (see Kowalchuk *et al.* 2010) are not found in northwestern North America, although they may be distributed in the extreme southwestern portion of YT. Also, assuming it is a valid taxon, the inland form found in the Yukon River basin of Alaska may have a wider distribution in south central YT including the Bell River basin of northern interior YT. These distributions are unconfirmed at present and this area is poorly surveyed particularly for water courses at high elevations.

Northern Dolly Varden exhibit sympatry in parts of their range but generally not syntopy with other char species as follows: a) Arctic Char in two lakes on North Slope YT isolated from the Firth River; and, b) Bull Trout in the Gayna River upstream in the Mackenzie River basin. Northern Dolly Varden and Lake Trout are widely sympatric and likely also syntopic in many areas, however, given that Lake Trout are primarily lake-associated and Dolly Varden are in high-gradient rivers, ecological preferences and habitat associations likely limit contacts between these two taxa.

6.2. BULL TROUT (FIGURE 2)

Bull Trout from interior North America (i.e., Idaho north to the Northwest Territories) are wholly freshwater in life history, however, similar to Dolly Varden they exhibit a variety of life history types (see Stewart *et al.* 2007). As noted above, Bull Trout and Dolly Varden were confused and the former was taxonomically submerged within the latter for long periods. Superficial resemblance between these two species is very high, however, recent research has confirmed that this southern taxon is found in southern YT and in the western portion of the NT in Mackenzie River drainages north to the central Sahtu Settlement Area (Reist *et al.* 2002). To date the northernmost location known is the Gayna River noted above (Mochnacz *et al.* 2009). This is the only location where Bull Trout and northern Dolly Varden are known to be sympatric but minimally syntopic. Additional sampling in suitable habitats surrounding this area is required to confirm this understanding.

Bull Trout and northern Dolly Varden distributions are parapatric in the NT; Bull Trout are not known to occur within the Peel River basin of central YT, however, adequate sampling to confirm this is required. Arctic Char and Bull Trout are allopatric. Similar to the situation described above, Bull Trout and Lake Trout are sympatric over wide areas but due to varying ecological preferences and habitat associations they exhibit minimal contact.

6.3. ARCTIC CHAR (FIGURE 3)

Arctic Char is a species primarily distributed in clear-flowing river and lake systems of the Canadian Arctic east of the Tuktoyaktuk Peninsula, and more particularly east of the Horton River. Coastal occurrences west of this area may represent either Arctic Char or possibly strays of Dolly Varden into this area. Upstream occurrences noted as points on Figure 3 represent unconfirmed, isolated (and presumably non-migratory) populations (e.g., point in the Anderson River basin) which, if correct, may be more widespread than presently understood. A stray of unknown origin has been recorded in Great Bear Lake (Reist unpubl. data), and Arctic Char originating from hatchery lineages have been stocked in closed lakes near Great Slave Lake (see Sawatzky *et al.* 2007). Arctic Char is found in two closely connected lakes (nos. 103/104) on the Yukon North Slope coastal plain immediately west of the Firth River. These populations which presently have no contact with Firth River Dolly Varden represent relictual forms of Arctic Char (Reist *et al.* 1997).

Although sympatric to a limited degree, northern Dolly Varden and Arctic Char are not syntopic. Arctic Char and Bull Trout are neither sympatric nor syntopic, and Arctic Char and Lake Trout are sympatric and generally syntopic over wide areas well east of the Mackenzie River basin.

6.4. LAKE TROUT (FIGURE 4)

Lake Trout are distributed throughout the whole area of the northwestern Arctic. As such they are sympatric with all of the other char species found in this area and in many cases will also be syntopic. As their name implies, Lake Trout are primarily associated with lakes but considerable diversity in life history is present and thus migrations through or habitat utilization of riverine environments may occur. This may, therefore, result in direct interactions among the species. In most cases such interactions are likely to be predatory in nature.

Lake Trout occur along the north slope of YT and in areas of the western Mackenzie Delta, however, most such occurrences are lacustrine. Thus, little direct contact between northern Dolly Varden and Lake Trout is likely. Far more likely are interactions and contact between Lake

Trout and the lacustrine life history type of Bull Trout, and between Lake Trout and Arctic Char, given the predilection of all three species to occupy lakes.

7.0. HYBRIDIZATION AND INTROGRESSION AMONG CHAR SPECIES

Hybridization (i.e., present-day inter-specific crosses) may be both an early warning of environmental disruption or population depletion, and also, if it occurs with significant frequency, a problem for the genetic integrity and recovery of depressed populations assuming the hybrids survive and are fertile (e.g., Rhymer and Simberloff 1996). Introgression (i.e., successful incorporation of foreign genotypes and/or characters into a species) is evidence of reproductively successful past hybridization events. Such events may have played a significant role in the evolution of northern fishes by transferring novel genotypes and characteristics among species (Wilson and Bernatchez 1998). Enhanced variability resulting from introgression presumably may confer some survival or adaptive advantage to individuals, and thus allow for persistence or proliferation of introgressed genotypes.

Sympatry and particularly syntopy raise the possibility for hybridization events among fish species, especially where habitat requirements are similar. Hybrids are usually recognized through some degree of character intermediacy. Introgression events are usually recognized through genetic criteria such as the presence of foreign alleles (e.g., for enzymes or microsatellites) or haplotypes (e.g., for mitochondrial DNA) in an individual assumed to be typical for another species. Although no specific examples of hybridization are directly documented among char taxa for the northwestern Arctic, there is evidence of some past possible hybridization/introgression events. Moreover, examples of hybridization and introgression among char species are known from other areas of North America, making the potential for hybridization in northern chars a real possibility in the northwestern Arctic particularly as aquatic ecosystems re-equilibrate from major stressors such as climate change.

Four taxa (northern DVCH, BUCH, ARCH and LKCH) yield six possible pairwise potential hybridizations. Evidence for such is summarized as follows.

1) DVCH x ARCH – Although no direct examples of northern Dolly Varden and Arctic Char hybridization exist, indirect evidence suggests such events have occurred in the past. Firstly, Reist *et al.* (1997) in examining allozyme variation in chars from the north slope noted almost complete fixation of alternative alleles between Arctic Char and Dolly Varden. The presence of Dolly Varden alleles in two fish which were morphologically Arctic Char and from a location in the central Arctic strongly implies a past introgression event between these two taxa. Secondly, Hamada *et al.* (1998) investigated SINEs (short interspersed nuclear elements) in the nuclear DNA of chars. These genetic markers are polymorphic within and among char taxa, and one potential explanation for such is the occurrence of introgressed individuals – however, this explanation was considered less likely than the alternative one of the maintenance of a polymorphic character that originated in their common ancestor in both Dolly Varden and Arctic Char lineages over evolutionary time. Finally, morphological intermediacy of some chars from Becharof Lake (southwestern Alaska) (Reist unpubl. data) where both Arctic Char and Dolly Varden (putative northern or intermediate form, Kowlachuk *et al.* 2010) co-occur suggests hybridization is possible for these two taxa.

2) DVCH x BUCH – No specific examples exist of this potential hybridization in northwestern Arctic North America. As noted above, the ranges of northern Dolly Varden and Bull Trout are parapatric (i.e., abut) in at least one area and one example of sympatry/syntopy is known along

the central Mackenzie River basin. Assuming northern and southern Dolly Varden are not substantively different, such hybridization is quite possible. That is, widespread hybridization and introgression of southern Dolly Varden with Bull Trout (putative western form) has been documented in BC where these taxa are sympatric and syntopic (Baxter *et al.* 1997). From 0-25% of samples from a large geographic area appeared to be hybrid individuals, suggesting widespread introgression occurs in this area (Redenbach and Taylor 2003). Interestingly, the direction of most introgression appeared to be from Bull Trout into Dolly Varden rather than the converse.

3) DVCH x LKCH – Literature searches were unsuccessful in documenting examples of this possible hybridization for either southern Dolly Varden and Lake Trout in northern BC, nor for northern Dolly Varden and Lake Trout in the northwestern Arctic. There appears to be no inherent reason why such could not occur, thus this absence of information is due to either the rarity of such events (e.g., due to ecological differences these fish rarely contact each other particularly at spawning time), to difficulties in recognizing such (i.e., poorly surveyed areas and field crews not attuned to such possibilities), or to both.

4) ARCH x LKCH – This hybridization and introgression is quite possible where the taxa co-occur, particularly east of the Mackenzie River basin. Genetic evidence indicates introgression between these two species (mtDNA from ARCH replacing that in LKCH) has occurred in the past (Wilson and Bernatchez 1998). Also, unconfirmed reports of this hybridization have been received from some Canadian Arctic locations (e.g., Stefansson Island (P. Wilkinson pers. comm.) and lakes on Melville Peninsula (C. Wilson pers. comm.)), however, no specimens have been examined and appropriate confirmatory studies are lacking.

5) BUCH x LKCH – Similar to the above summary for Dolly Varden and Lake Trout hybridization, although theoretically possible no examples of such are known likely for the same reasons.

6) ARCH x BUCH – These species are presently not sympatric thus hybridization between these can not occur under present circumstances.

8.0. CHARS FROM THE CORONATION GULF AREA

As noted above, all chars (i.e., excluding Lake Trout) distributed in Arctic North America east of the Mackenzie River basin have generally been assumed to represent populations of Arctic Char (i.e., following McPhail 1961, eastern form Arctic Char). No substantive taxonomic research on char diversity in this area has been conducted since McPhail's summary, however, recent work on chars from the Coronation Gulf area suggests a complex circumstance is present (Reist *et al.* unpubl. data). That is, various rivers systems in this area from Coppermine River in the west to Tree River in the east (and perhaps other systems in intervening areas), appear to have a taxon present resembling Dolly Varden and co-occurring with what appear to be typical Arctic Char. Unlike the situation described above for the north slope Yukon and western Mackenzie Delta, rivers in this area are both fast-flowing characterized by clear water, but also drain substantive lake systems. That is, habitats relevant to a riverine char such as a Dolly Varden-like taxon and those relevant to a lacustrine char such as Arctic Char are both present in these systems. From west to east these rivers include the Coppermine, Kagaryuak and Tree rivers; Arctic Char appears to be the only taxon from this complex present in rivers systems further to the west and east of this area. Morphological (meristic and morphometric) evidence (i.e., the same characters used by Reist *et al.* 1997 to differentiate northern Dolly

Varden and Arctic Char) suggests that char from the Coppermine River are a mixture of both possible char taxa, those from the Kagaryuak River are primarily Arctic Char, and those from Tree River mostly resemble Dolly Varden. Mitochondrial DNA genetic evidence suggests fish from the Coppermine River have mostly Arctic Char haplotypes although about 19% have Dolly Varden haplotypes; fish from the Kagaryuak River have mostly Arctic Char haplotypes (~12% Dolly Varden haplotypes); and, fish from Tree River have mostly Dolly Varden haplotypes (~74%). The situation here is clearly complex and the possibilities include the following: a) two co-occurring char taxa are present to varying abundances in the various rivers and associated lakes (i.e., putatively northern Dolly Varden and eastern form Arctic Char) and they maintain their respective specific integrities; b) an introgressed complex of char is present in this area with some individuals morphologically and genetically (mtDNA) resembling either of the putative parental taxa; and, c) two distinct ecological forms of eastern Arctic Char are present, one of which converges upon northern Dolly Varden in morphology and with respect to some genetic characters. Present data (ecological, morphological, and mtDNA genetic) can not discriminate among these possibilities, however, studies of nuclear microsatellite DNA are underway to address this question. Because this situation is un-resolved and poorly known at present, these populations of a putative northern form Dolly Varden-like char are not considered herein to represent this taxon and thus should not be included in analyses relevant to the status assessment of northern Dolly Varden. In the event that possibility a) above is the case, then these locations would represent widely disjunct and outlying populations of northern Dolly Varden and likely merit special status assignment.

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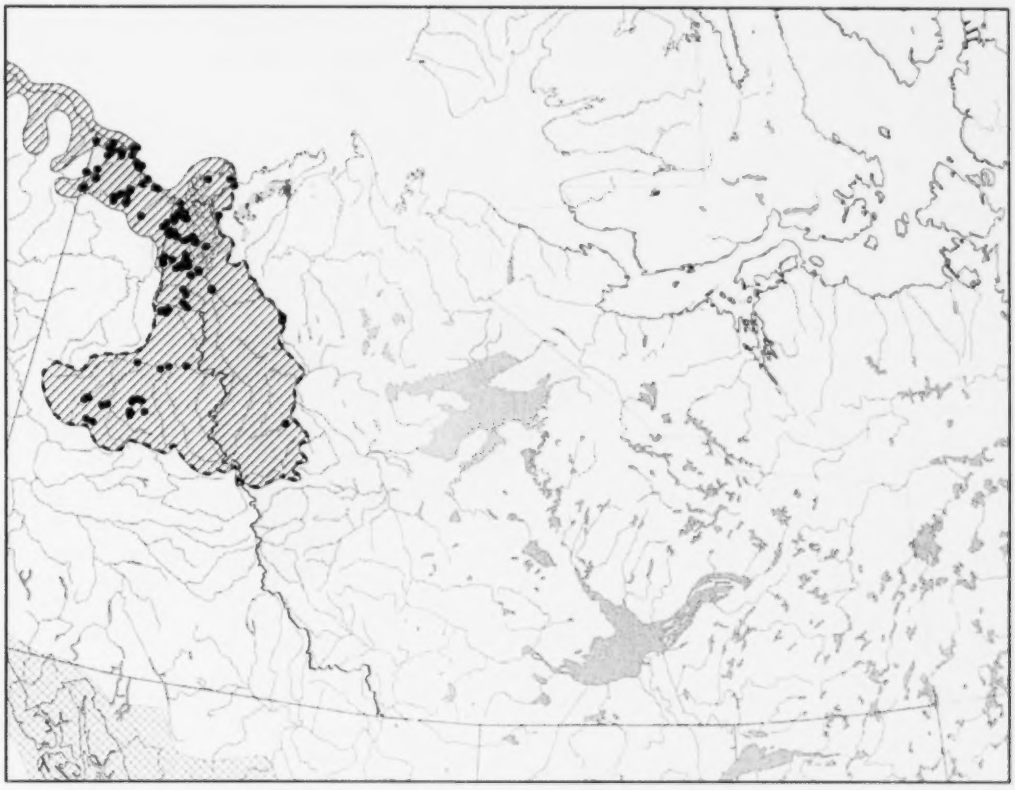

Figure 1. Generalized distribution of northern Dolly Varden (single line hachures) in northwestern Arctic Canada (after Sawatzky *et al.* 2007). Points indicate confirmed locations for Dolly Varden, however, interior points in the Peel River basin (YT) may represent an interior form rather than the northern form. Dashed boundaries indicate presumed (but unconfirmed) extent of distribution. Distribution of southern Dolly Varden (cross-hachuring) is shown for northern BC (after McPhail 2007). Note that southern Dolly Varden do not occur in drainages east of the continental divide, nor is this taxon present in the southern YT (Haas and McPhail 1991).

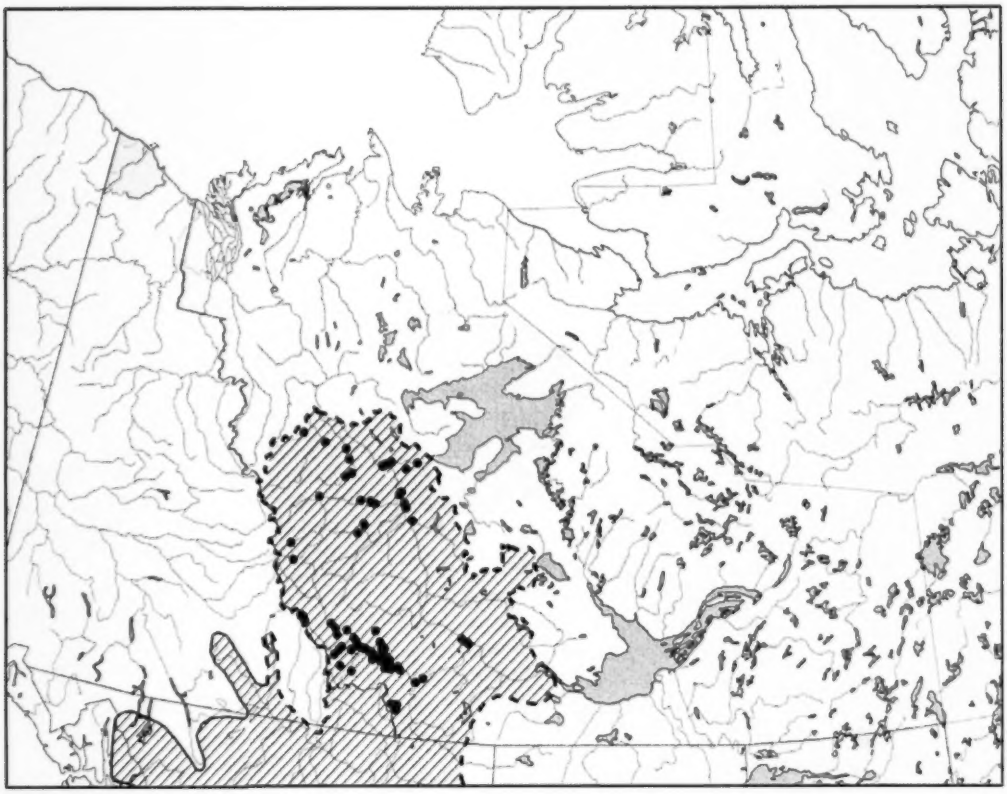

Figure 2. Generalized distribution of Bull Trout (hachuring) in northwestern Arctic Canada (after Sawatzky *et al.* 2007). Points indicate confirmed locations for Bull Trout, many of which were re-interpreted as such from previous identifications to different taxa by Reist *et al.* (2002). Dashed boundaries indicate presumed (but unconfirmed) extent of distribution.

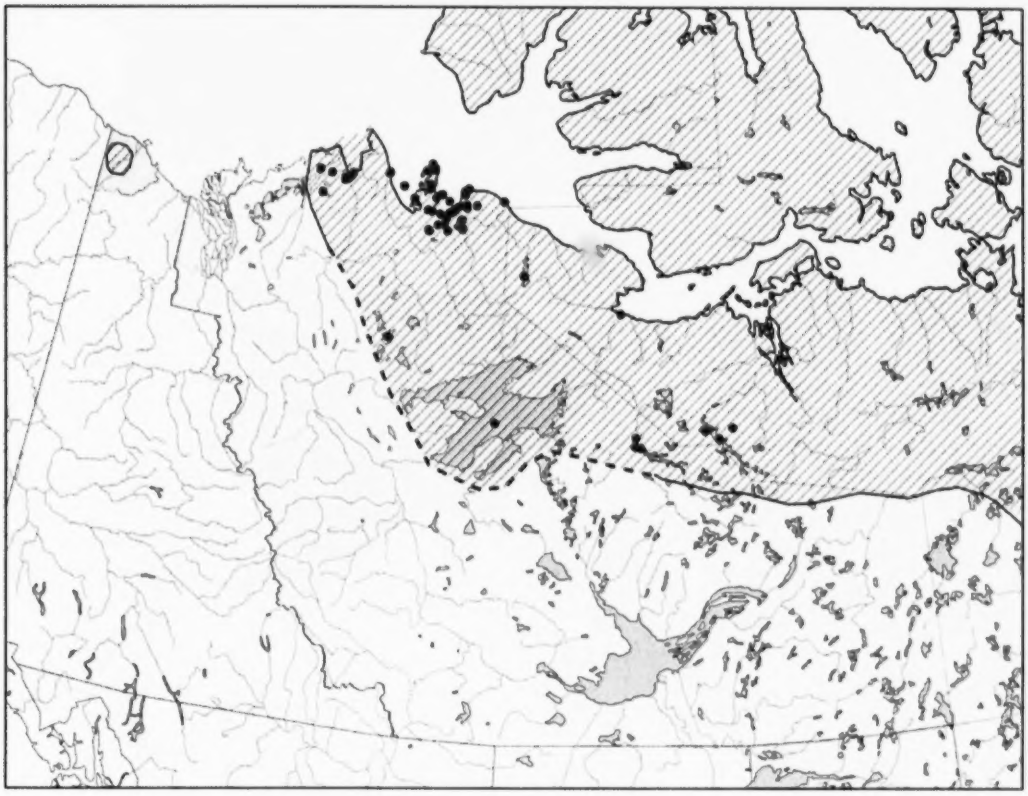

Figure 3. Generalized distribution of Arctic Char (hachuring) in northwestern Arctic Canada (after Sawatzky *et al.* 2007). Points indicate confirmed locations for Arctic Char. The interior point in the Great Bear Lake represents a stray. Dashed boundaries indicate presumed (but unconfirmed) extent of distribution, which excluding this stray is likely outside all Mackenzie River basin drainages including Great Bear Lake. The occurrence area in extreme northwestern Yukon is not to scale but Arctic Char are confirmed in lakes 103 and 104.

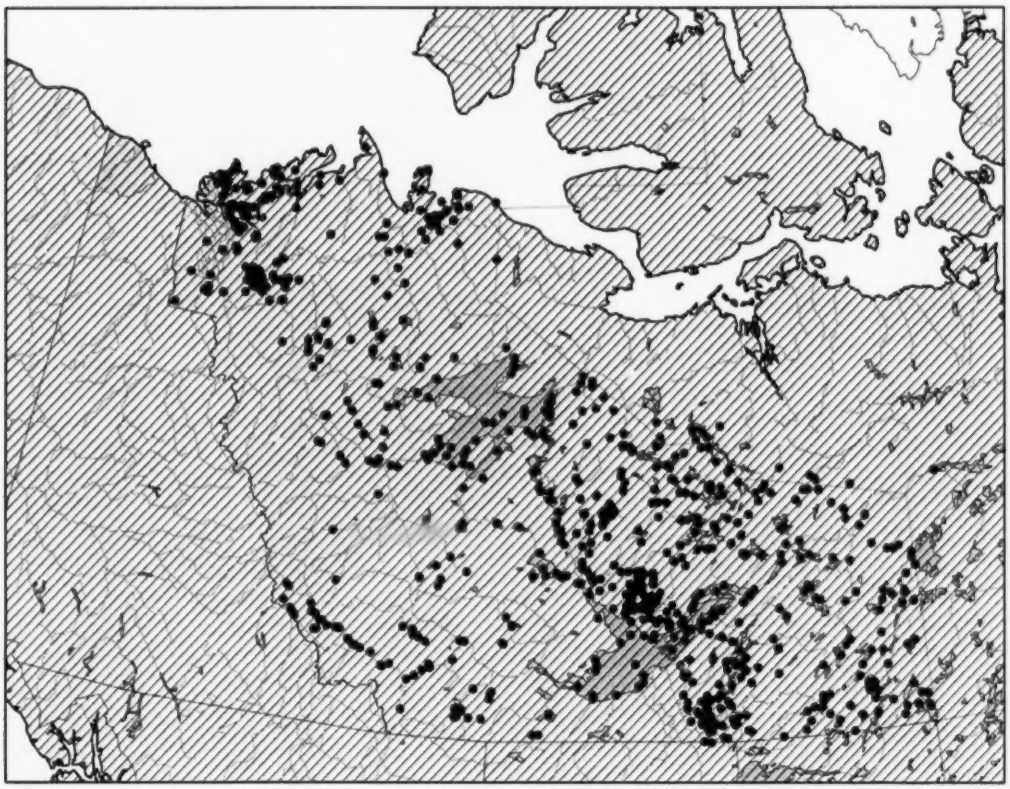

Figure 4. Generalized distribution of Lake Trout (hachuring) in northwestern Arctic Canada (after Sawatzky *et al.* 2007). Points indicate confirmed locations for Lake Trout in mainland NT.